Reference: *Biol. Bull.* 177: 287–294. (October, 1989)

Population Genetics of the Common Squid *Loligo pealei* LeSueur, 1821, from Cape Cod to Cape Hatteras

RONALD L. GARTHWAITE[1], CARL J. BERG JR.[2], AND JUNE HARRIGAN[3]

Marine Biological Laboratory, Woods Hole, Massachusetts 02543

Abstract. Collections of *Loligo pealei* LeSueur, 1821 from the Atlantic seaboard between Cape Hatteras and Georges Bank differ significantly in both allele and genotype frequencies at the phosphoglucomutase locus. *Loligo pealei* collected off the coast of Virginia are distinct at this locus from all other areas surveyed. *Loligo pealei* collected from Georges Bank also differ significantly at this locus from those collected inshore off Cape Cod. These results suggest that *L. pealei* along the Atlantic seaboard consists of several distinct populations. A comparison of allele frequencies at nine allozyme loci among *L. pealei, Loligo plei* Blainville, 1823, and *Lolliguncula brevis* (Blainville, 1823) reveals that *L. pealei* differs completely from *L. plei* at five loci, *L. pealei* from *L. brevis* at six loci, and *L. plei* from *L. brevis* at three loci.

Introduction

Data collected over the past one hundred years still present a confused picture of the stock[4] characteristics of the common squid *Loligo pealei* LeSueur, 1821. The existence of two major discrete "groups" and a third "mixed group" has been demonstrated repeatedly in size frequency data from squid caught in the region extending from Georges Bank to Cape Hatteras. This size structure has been explained by invoking different sub-species (Verrill, 1882), brood stocks (Summers, 1971), or alternate generations (Mesnil, 1977). In addition, there is some uncertainty as to how many species this taxon represents throughout its range (Cohen, 1976; Summers, 1983). In reviewing the assumptions needed for statistical analysis of population structure based on size frequency distributions, Summers (1983) points out that *L. pealei* is not homogeneous either throughout its latitudinal range, across the continental shelf, through time at a single station, or even between successive tows. All of these data suggest that there are genetically discrete populations which are isolated by seasonal or geographic spawning differences. The single fishery "stock" or "population" of *L. pealei* on the eastern seaboard (*e.g.*, Lange and Sissenwine, 1980, 1983) probably consists of several stocks or populations.

To date, biochemical genetic data have not been applied to the problem of stock structure in *Loligo pealei*. In this study we used allozyme data to clarify the population or stock structure of this species along the northeastern coast of the United States. In the process, we also present a biochemical genetic comparison of *L. pealei* with the morphologically similar *Loligo plei* Blainville, 1823, and with *Lolliguncula brevis* (Blainville, 1823).

Materials and Methods

Squid were collected by trawl nets from research vessels of the Marine Biological Laboratory and the Northeast Fisheries Center of the United States National Marine Fisheries Service (NMFS). Collection data for the trawl stations are listed in Table 1. The location of these stations is illustrated in Figure 1. For purposes of analysis, mainly to increase sample sizes, these trawl samples were grouped into six regions [North Carolina, Virginia, Delaware, Woods Hole, Cape Cod, and Georges Bank (Table 1)], which we subsequently treated as six separate samples. With the exception of station 45, stations were

Received 3 October 1988; accepted 31 July 1989.

[1] Present address: Institute of Marine Sciences, University of California, Santa Cruz, CA 95064.

[2] Present address: Florida Department of Natural Resources, Marine Research Institute, 13365 Overseas Highway, Marathon, FL 33050.

[3] Present address: Department of Ocean Engineering, University of Hawaii, Honolulu, HI 96822.

[4] In this paper we use the term "stock" as defined by Ihssen *et al.* (1981): "An intraspecific group of randomly mating individuals with temporal or spatial integrity."

Table I

Collection data for squid samples used in this study

Region	NMFS station	Date	Depth (m)	Approximate Latitude	Approximate Longitude	# of *Loligo pealei* surveyed	Other species present
North Carolina	34	2 OCT 85	36–43	35°41′	75°06′	32	*L. plei*
	35	2 OCT 85	58–63	35°44′	74°56′	24	
Virginia	45	3 OCT 85	16–15	36°28′	75°48′	16	
	53	4 OCT 85	25–24	37°25′	75°25′	54	*L. plei*
	56	4 OCT 85	14	37°45′	75°27′	9	*L. brevis*
	57	4 OCT 85	19	37°54′	75°11′	10	
	58	4 OCT 85	23–25	37°57′	75°02′	20	
Delaware	83	6 OCT 85	192–197	38°32′	73°16′	75	
	85	6 OCT 85	64–67	38°52′	73°21′	40	
Woods Hole		OCT 84	10–20	41°30′	70°30′	110	
		MAY 85	10–20	41°30′	70°30′	120	
		OCT 85	10–20	41°30′	70°30′	100	
Cape Cod	371	7 NOV 85	29–33	41°57′	69°56′	48	
	372	7 NOV 85	32–34	41°59′	69°57′	137	
Georges Bank	198	21 OCT 85	99	40°42′	67°15′	199	

NMFS = National Marine Fisheries Service. See Figure 1 for station locations.

grouped on the basis of physical proximity. Station 45, which lies approximately half way between the North Carolina stations and the other Virginia stations (Fig. 1), was grouped with the Virginia stations because it represents a similar, near-shore, shallow-water habitat (Table I). The three samples collected off Woods Hole represent three different year classes (1983, 1984, and 1985). Squid collected in October of 1984 and 1985 were juveniles that hatched during the preceding summers, while the sample from May 1985 consisted of breeding adults most likely hatched in 1983.

Soon after collection, a piece of mantle tissue was removed from each animal and frozen in liquid nitrogen for later electrophoretic analysis. The remainder of each squid was then frozen at −20°C. These specimens were later thawed and their mantle lengths measured to the nearest mm using a meter ruler.

Tissue samples for electrophoresis were returned to the laboratory and stored at −70°C until analyzed. Before electrophoretic analysis, these tissue samples were sonicated on ice in approximately equal weight to volume of 0.05 *M* Tris-HCl pH 7.5 and centrifuged for 15 min in a clinical centrifuge at 2°C. Horizontal starch gel electrophoresis (Sigma starch) using filter paper wicks (Whatman #2) and buffer systems two and five of Selander *et al.* (1971) was used to determine allele frequencies in the collections at 19 biochemical loci. Buffer system two was used to survey the collections for aminopeptidase (AP), leucine aminopeptidase-1 (LAP-1), leucine aminopeptidase-2 (LAP-2), malic enzyme (ME), phosphoglucomutase (PGM), phosphoglucose isomerase-1 (PGI-1), phosphoglucose isomerase-2 (PGI-2), superoxide dismutase (SOD), and xanthine dehydrogenase (XDH). Buffer system five was used to survey the collections for α-glycerophosphate dehydrogenase (α-GPDH), alcohol dehydrogenase (ADH), esterase (EST), glutamate oxaloacetate transaminase-1 (GOT-1), glutamate oxaloacetate transaminase-2 (GOT-2), isocitrate dehydrogenase (IDH), malate dehydrogenase-1 (MDH-1), malate dehydrogenase-2 (MDH-2), nothing dehydrogenase (NDH), and sorbitol dehydrogenase-1 (SDH-1). Initially, 40 specimens of *Loligo pealei* from Woods Hole were surveyed for all 19 loci. Nine of these loci (PGM, ME, MDH-1, MDH-2, IDH, GOT-1, GOT-2, PGI-1, and PGI-2) were chosen for use in the larger survey. Enzyme stain recipes were taken from Shaw and Prasad (1970) and Ahmad *et al.* (1977) with minor modification.

Differences in size frequency distributions among trawl samples and among individuals possessing various alleles within trawl samples were tested for significance using F-tests on variances and t-tests on means. Allele frequency differences among stations and regions were tested for significance using the tables of Mainland *et al.* (1956). Genotype frequency differences among stations and regions were tested for significance using G tests on contingency tables (Sokal and Rohlf, 1969).

During our survey, we encountered one species of squid that was morphologically distinct from *Loligo*

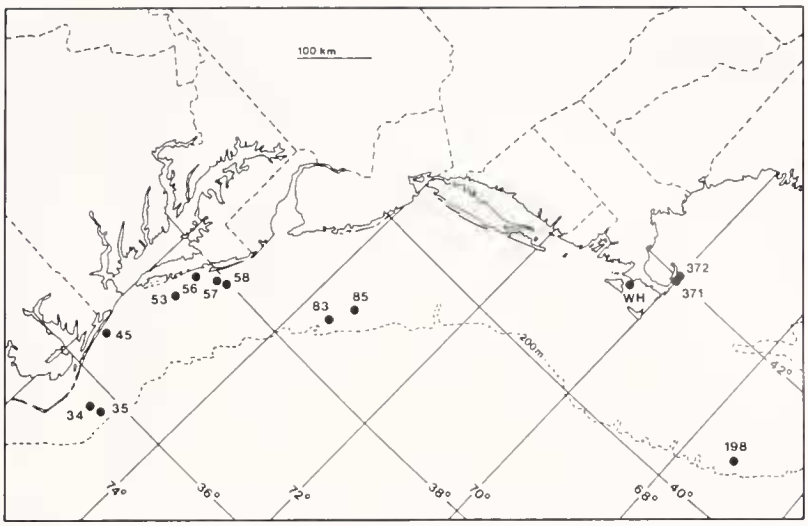

Figure 1. The location of the National Marine Fisheries Service trawl stations from which squid used in this study were collected. See Table I for collection data. WH = Woods Hole, MA.

pealei and another that was electrophoretically distinct from *L. pealei*. We suspected that these squid were *Lolliguncula brevis* and *Loligo plei*, respectively. *Loligo plei* is morphologically very similar to *L. pealei*, and the two species are not easily separated on morphological grounds (Cohen, 1976; Whitaker, 1980; Summers, 1983; Hanlon, 1988). Since the ranges of *L. pealei* and *L. plei* overlap in our study area (Whitaker, 1980), it is important that we demonstrate that we can consistently identify *L. plei* electrophoretically and that we have not accidentally included specimens of this species in our study of *L. pealei*. To confirm the identities of these species in our collections we obtained known specimens of *L. plei* and *L. brevis* from Dr. Roger Hanlon of Galveston, Texas. These Texas specimens were compared directly, on the same gels, to our specimens of *L. pealei*, *L. plei*, and *L. brevis* for the nine loci listed above.

Results

Population genetics of Loligo pealei

Significant variation in squid size distributions existed among trawl samples both within and among regions. Out of a total of 55 pair-wise comparisons among the 11 trawl samples taken in October 1985, all but 5 were significantly different in variance or mean size ($P < .05$).

Banding patterns for all loci surveyed conformed to Mendelian expectations (Harris and Hopkinson, 1976). Heterozygotes for PGM were found in both males and females, indicating that this locus is not sex linked. Alleles, allele frequencies, and sample sizes for the collections of *Loligo pealei* from all six regions are listed in Table II. Phosphoglucomutase genotype frequencies for all regions are given in Table III.

On the whole, *Loligo pealei* possessed very low levels of genetic variation. Of the 19 loci surveyed, variant alleles were found only in PGM, ME, MDH-2, IDH, GOT-1, and PGI-2. However, of these six loci, the frequencies of the variant alleles were 1% or less in all but PGM for which the maximum frequency of variant alleles in any region surveyed was only 7.5% (Georges Bank, Table II). Combining the data over all collections, only 5% of all loci surveyed in *L. pealei* were polymorphic at the 1% level and the average heterozygosity per individual was only 0.6%.

Given the low levels of genetic variation present in the collections of *Loligo pealei* surveyed, it is unlikely that differences in allele frequencies among the collections will be significant. Only PGM is polymorphic enough to reasonably give significant results with these sample sizes. No significant differences in allele or genotype frequencies were found among stations within regions for any locus. Among the three Woods Hole collections, which represent squid hatched in three different years (1983, 1984, and 1985) no significant differences in allele or genotype frequencies were found at any locus.

Individuals possessing allelic variants generally did not differ significantly in size from other squid from the same trawl; the exceptions being squid possessing PGM allele 1.18 from Georges Bank, which had a significantly larger mean length than squid which did not possess this allele ($P < .05$), and squid possessing ME allele 1.05 at Georges Bank and PGM allele 1.18 at Woods Hole (May 1985), which both had significantly larger variances than the remaining squid in each sample ($P < .05$).

Table II

Allele frequencies, and sample sizes in number of alleles surveyed (in parentheses) for collections of Loligo pealei *from the northwest Atlantic. Alleles are expressed as migration rate relative to the most common allele*

Locus	Allele	North Carolina	Virginia	Delaware	Woods Hole			Woods Hole total	Cape Cod	Georges Bank
					OCT 84	MAY 85	OCT 85			
PGM	(N)	(112)	(218)	(230)	(220)	(240)	(200)	(660)	(370)	(398)
	1.18	.054	—	.030	.036	.021	.030	.029	.022	.030
	1.00	.928	.972	.948	.946	.962	.950	.953	.967	.925
	.78	.018	.028	.022	.018	.017	.020	.018	.011	.045
ME	(N)	(112)	(146)	(164)	(220)	(240)	(200)	(660)	(370)	(398)
	1.05	—	—	—	—	—	—	—	—	.008
	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.992
MDH-2	(N)	(112)	(120)	(92)	(220)	(240)	(200)	(660)	(370)	(398)
	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.997	1.000
	.64	—	—	—	—	—	—	—	.003	—
IDH	(N)	(112)	(100)	(102)	(220)	(240)	(200)	(660)	(370)	(398)
	1.17	—	—	—	—	.004	—	.002	.005	—
	1.00	1.000	1.000	1.000	1.000	.996	.990	.995	.992	1.000
	.88	—	—	—	—	—	.010	.003	—	—
	.69	—	—	—	—	—	—	—	.003	—
GOT-1	(N)	(112)	(136)	(150)	(160)	(240)	(200)	(600)	(370)	(398)
	1.16	—	—	—	—	—	—	—	—	.003
	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.992
	.79	—	—	—	—	—	—	—	—	.005
PGI-2	(N)	(112)	(126)	(122)	(220)	(240)	(200)	(660)	(370)	(398)
	1.00	1.000	1.000	1.000	1.000	.996	1.000	.998	1.000	1.000
	.68	—	—	—	—	.004	—	.002	—	—
MDH-1	(N)	(112)	(120)	(92)	(220)	(240)	(200)	(660)	(370)	(398)
	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GOT-2	(N)	(112)	(74)	(150)	(160)	(240)	(200)	(600)	(370)	(398)
	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGI-1	(N)	(112)	(126)	(122)	(220)	(240)	(200)	(660)	(370)	(398)
	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Among all pair-wise comparisons of squid collections (with the three Woods Hole collections combined and treated as a single sample), the Virginia sample stands out as being significantly different from the North Carolina sample ($P < .05$) and the Woods Hole sample ($P < .05$) in the frequency of PGM allele 1.18. In PGM ge-

Table III

Phosphoglucomutase genotype frequencies for collections of Loligo pealei *from the northwest Atlantic*

Region	Sample size	PGM genotype				
		1.18/1.00	1.18/.78	1.00/1.00	1.00/.78	.78/.78
North Carolina	56	.107	—	.857	.036	—
Virginia	109	—	—	.945	.055	—
Delaware	115	.061	—	.896	.043	—
Woods Hole						
OCT 1984	110	.064	.009	.900	.027	—
MAY 1985	120	.042	—	.925	.033	—
OCT 1985	100	.060	—	.900	.040	—
Total	330	.055	.003	.909	.033	—
Cape Cod	185	.043	—	.935	.022	—
Georges Bank	199	.060	—	.855	.080	.005

notype frequencies, the Virginia sample is significantly different from the samples from all other regions ($P < .05$). In addition, the Georges Bank sample is significantly different from its nearest neighbor, Cape Cod, in PGM genotype frequencies ($P < .05$). All other pair-wise comparisons of regions for PGM and all other loci gave nonsignificant results for both allele and genotype frequencies.

Taxonomy

Alleles, allele frequencies, and sample sizes for the comparison of allele frequencies in *Loligo pealei, Loligo plei,* and *Lolliguncula brevis* are listed in Table IV. Our specimens of *L. plei* and *L. brevis* were electrophoretically identical to the Texas specimens of these species for all loci surveyed.

Sample sizes for *Loligo plei* and *Lolliguncula brevis* were small (eight individuals apiece) and alleles with frequencies lower than approximately 6% were not likely to have been detected. However, all loci surveyed, with the exception of IDH, PGI-2, and MDH-1, showed fixed allelic differences among species such that individuals of all three species can be identified easily and unambiguously solely on the basis of the alleles they possess at these diagnostic loci. *Loligo pealei* differs completely from *L. plei* at five loci, *L. pealei* from *L. brevis* at six loci, and *L. plei* from *L. brevis* at three loci (Table IV). Nei's genetic distances (Nei, 1972) for pair-wise comparisons of the three species are: .81 for *L. pealei vs. L. plei,* 1.10 for *L. pealei vs. L. brevis,* and .40 for *L. plei vs. L. brevis.*

Discussion

Generally, biochemical genetic data, of the kind reported here, are much more appropriate and effective in determining population or stock structure than are size frequency data (Ihssen *et al.,* 1981). Size and growth rate are both affected by numerous environmental factors such as temperature and food quality or availability (Hixon, 1983; Ihssen *et al.,* 1981). Thus individuals from the same population or stock can differ significantly in these measures if they experience different environments. This is particularly a problem with *Loligo pealei,* which appears to have a rather extended spawning and hatching period (Summers, 1971; Lange and Sissenwine, 1980, 1983). Biochemical genetic data are typically not *directly* affected by the environment and thus serve as a permanent and direct measure of genetic relatedness among collections or populations (Ihssen *et al.,* 1981; Avise, 1974; Ayala, 1983). This technique has, therefore, shifted from an optional to a primary position among methods used in studies of population or stock structure (Ihssen *et al.,* 1981).

The low level of genetic variation found here in *Loligo pealei* limits the effectiveness of this technique in determining population structure in this species since only one locus (PGM) was polymorphic enough to detect differentiation among collections with reasonable sample sizes. Nevertheless, for this locus, significant differentiation was detected among collections. The patterning of this differentiation suggests that *L. pealei* in the northwest Atlantic is comprised of at least three populations. Genetically, the Virginia sample is distinct from samples from all other regions included in this study and the Georges Bank sample is distinct from its nearest neighbor, Cape Cod. However, given that *L. pealei* are migratory and highly mobile (Lange and Sissenwine, 1983), it is unlikely that the spatial arrangement of these populations is constant.

Previous studies on the population or stock structure of *Loligo pealei,* based on size frequency distributions, have postulated two groups of squid which may or may not be genetically isolated (Verrill, 1882; Summers, 1971; Mesnil, 1977; Lange and Sissenwine, 1980, 1983). We can find little genetic evidence for this structure. In no trawl sample was there an obvious bimodality in size frequency distributions. Nor did we find significant gene frequency differences among the three Woods Hole collections. While we found exceptional amounts of variation among trawl samples in size frequency distributions, there is no overall correlation between mean size and PGM gene frequency ($r^2 = .02$, $P < .05$). The fact that the Virginia trawl samples (which are genetically coherent and, as a whole, distinct from all other regions) are heterogeneous in size frequency ($P < .05$) indicates that size frequency is not a good indicator of population structure in *L. pealei.* It is possible that size frequency differences among samples are due to differences in environmental factors experienced by different groups of squid or differences in sex ratio among groups [male *L. pealei* tend to grow larger than females (Mesnil, 1977)]. Whether size frequency differences are due to environmental differences, sex ratio differences, or differences in spawning time, they do not seem to be associated with significant restrictions in gene flow.

The differences in size distributions between individuals possessing different alleles that was found in several trawl samples is interesting, but the small number of allelic variants obtained in any one sample makes analysis difficult. These differences in size distributions may be a result of selective forces acting on alleles or may indicate that our trawl samples were composed of a mixture of squid populations which differ in both size and allele frequency. In this latter case, this data would be evidence for the population structure postulated by previous workers (Verrill, 1882; Summers, 1971; Mesnil, 1977).

The degree of interpopulational genetic differentiation reported here is almost certainly a minimum value for

Table IV

Allele frequencies at nine loci in three species of squid

Locus	Allele	*Loligo pealei* (1704)	*Loligo plei* (16)	*Lolliguncula brevis* (16)
PGM	1.18	.026	—	—
	1.00	.950	—	—
	.78	.024	—	—
	.60	—	1.000	1.000
ME	1.05	.002	—	—
	1.00	.998	—	—
	.95	—	1.000	1.000
MDH-2	1.00	.999	1.000	—
	.90	—	—	1.000
	.64	.001	—	—
IDH	1.17	.002	—	—
	1.00	.996	1.000	1.000
	.88	.001	—	—
	.69	.001	—	—
GOT-1	1.16	.001	—	—
	1.00	.998	—	—
	.88	—	—	1.000
	.85	—	1.000	—
	.79	.001	—	—
PGI-2	1.00	.999	1.000	1.000
	.68	.001	—	—
MDH-1	1.00	1.000	1.000	1.000
GOT-2	1.00	1.000	—	—
	.86	—	—	1.000
	*	—	1.000	—
PGI-1	1.00	1.000	—	—
	.74	—	1.000	1.000

Minimum sample sizes (in number of alleles surveyed) are in parentheses. Alleles are expressed as migration rate relative to the most common *Loligo pealei* allele. * = no activity.

Loligo pealei. All of the collections of *L. pealei* surveyed in this study came from a limited biogeographic range extending north from Cape Hatteras to Cape Cod. The range of *L. pealei* extends south as far as the Gulf of Venezuela (Cohen, 1976; Summer, 1983) and it may be expected that comparisons of populations north of Cape Hatteras with those south of Cape Hatteras or from the Gulf of Mexico may reveal additional genetic differentiation since Cape Hatteras and Florida form natural boundaries for many other species (Briggs, 1974).

The low levels of intrapopulational genetic variation in *Loligo pealei* found in this study seem to be a general characteristic of squid. Similar low levels of genetic variation have been reported for *Loligo opalescens* Berry, 1911 (Christofferson *et al.*, 1978; Augustyn and Grant, 1988), *Loligo vulgaris* Lamarck, 1798 (Augustyn and Grant, 1988), and *Illex illecebrosus* (LeSueur, 1821) (Romero and Amaratunga, 1981). In addition, even though our data are limited both in number of loci (9) and number of individuals (8) surveyed, *Loligo plei* and *Lolliguncula brevis* also appear to fit this pattern since allelic variants for the loci surveyed here, if present at all, would likely be in frequencies of 6% or less. Table V presents a comparison of measures of genetic variation based on data taken from the literature for several squid species and for invertebrates in general.

While the lack of genetic variation in squid may limit the use of this kind of data in studies of population structure, it makes it that much more useful in taxonomic studies since banding patterns are simpler and intraspecific variation is minimized. In this study, we found biochemical data to be an excellent taxonomic tool. While *Loligo pealei* and *Loligo plei* are morphologically very similar and difficult to differentiate on morphological grounds (Cohen, 1976; Whitaker, 1980; Summer, 1983; Hanlon, 1988), they are quite distinct biochemically (differing completely at five out of nine loci) and easily distinguishable from one another. In addition, both species are easily distinguishable electrophoretically from *Lolliguncula brevis.* That *L. plei* appears to be more closely related to *L. brevis* than *L. pealei* is unexpected and interesting but this result may be an artifact of the small number of loci surveyed.

Several other studies of squid population structure and taxonomy have been performed using biochemical genetic data. Two of these studies (Ally and Keck, 1978; Christofferson *et al.*, 1978) are concerned with *Loligo opalescens* along the California coast, and both suggest a separate southern population on the basis of biochemical data. This population structure for *L. opalescens* is substantiated by data on spawning peaks (Fields, 1965) and morphological indices (Kashiwada and Recksiek, 1978). A third study concerns *Illex illecebrosus* off the eastern coast of Canada (Romero and Amaratunga, 1981). In this study, no significant differences were detected among collections, but this is not surprising considering the limited geographical range over which the collections were taken and the fact that sample sizes were small. Smith *et al.* (1981) studied *Nototodarus sloani* Gray, 1849, in New Zealand. On the basis of mainly electrophoretic evidence, Smith *et al.* found that what was previously thought to be eight sub-populations of *N. sloani* instead consisted of two species that are largely non-overlapping in their distributions. This conclusion concerning *N. sloani* was substantiated by data on morphology and parasite load. Finally, Augustyn and Grant (1988), in their morphological and biochemical study of African squid, discovered that what had previously been considered two separate species on morphological grounds (*Loligo vulgaris* and *Loligo reynaudii* d'Orbigny, 1845) actually consisted of two subspecies of *L. vulgaris* as demonstrated by biochemical data.

Table V

Genetic variability in squid

	# of Loci surveyed	# of Individuals surveyed per locus	% Polymorphic loci (1% level)	Average Ho	Average Ne	Reference
Illex illecebrosus	11	10–156	9	.005	1.01	Romero and Amaratunga, 1981
Loligo opalescens	30	45	17	.037	1.06	Augustyn and Grant, 1988
Loligo pealei	19	40–994	5	.006	1.01	This paper
Loligo plei	9	8	0	.000	1.00	This paper
Loligo vulgaris reynaudii	30	44	23	.030	1.05	Augustyn and Grant, 1988
Loligo vulgaris vulgaris	30	15	7	.011	1.01	Augustyn and Grant, 1988
Lolliguncula brevis	9	8	0	.000	1.00	This paper
Average for other invertebrates			38	.100	1.11	Nevo *et al.*, 1984

Values for *Loligo pealei* and *Illex illecebrosus* are for combined data over several collections. Ho = observed heterozygosity, Ne = effective number of alleles.

Thus, on the whole, biochemical genetic studies have proven to be very useful in the study of squid stock and population structure, furnishing data on the number of species present (Smith *et al.*, 1981; Augustyn and Grant, 1988) and the spatial distribution of breeding units within these species (Ally and Keck, 1978; Christofferson *et al.*, 1978; this paper). Obviously, this sort of information should be of central importance to fisheries management because, to use a fishery stock effectively, the number of species present, their spatial distributions, and their population structure must be considered.

Acknowledgments

This project was made possible through a collaboration of scientists and staff of the United States National Marine Fisheries Service, Northeast Fisheries Center and the Marine Biological Laboratory, both in Woods Hole, Massachusetts. We thank Y. P. Wang for technical assistance. Dr. R. T. Hanlon kindly supplied specimens through DHHS Grant RR01024. This project was supported in part by a grant from the Charles Ulrick and Josephine Bay Foundation to Dr. Garthwaite.

Literature Cited

Ahmad, M., D. O. F. Skibinski, and J. A. Beardmore. 1977. An estimate of the amount of genetic variation in the common mussel *Mytilus edulis*. *Biochem. Genet.* **15:** 833–846.

Ally, J. R. R., and S. A. Keck. 1978. A biochemical-genetic population structure study of market squid, *Loligo opalescens*, along the California coast. *Calif. Dept. Fish Game Fish Bull.* **169:** 113–121.

Augustyn, C. J., and W. S. Grant. 1988. Biochemical and morphological systematics of *Loligo vulgaris vulgaris* Lamarck and *Loligo vulgaris reynaudii* D'Orbigny NOV. COMB. (Cephalopoda: Myopsida). *Malacologia* **29:** 215–233.

Avise, J. C. 1974. Systematic value of electrophoretic data. *Syst. Zool.* **23:** 465–481.

Ayala, F. J. 1983. Enzymes as taxonomic characters. Pp. 3–26 in *Protein Polymorphism: Adaptive and Taxonomic Significance*, G. S. Oxford and D. Rollinson, eds. Academic Press, New York.

Berry, S. 1911. Notes on some cephalopods in the collection of the University of California. *Univ. Calif. Publ. Zool.* **8:** 301–310.

Blainville, H. 1823. Mémoire sur les espèces du genre calmar (*Loligo*, Lamarck). *J. Physique Chimie d'Histoire Naturelle* **96:** 116–135.

Briggs, J. C. 1974. *Marine Zoogeography*. McGraw Hill, New York. 475 pp.

Christofferson, J. P., A. Foss, W. E. Lambert, and B. Welge. 1978. An electrophoretic study of select proteins from the market squid, *Loligo opalescens* Berry. *Calif. Dept. Fish Game Fish Bull.* **169:** 123–133.

Cohen, A. C. 1976. The systematics and distribution of *Loligo* (Cephalopoda, Myopsida) in the western North Atlantic, with descriptions of two new species. *Malacologia* **15:** 299–367.

Fields, W. G. 1965. The structure, development, food relations, reproduction, and life history of the squid, *Loligo opalescens* Berry. *Calif. Dept. Fish Game Fish Bull.* **131:** 1–108.

Gray, J. E. 1849. Catalogue of the mollusca in the collection of the British Museum. Pt. 1. Cephalopoda Antepedia. British Museum, London.

Hanlon, R. T. 1988. Behavioral and body patterning characters useful in taxonomy and field identification of cephalopods. *Malacologia* **29:** 247–264.

Harris, H., and D. A. Hopkinson. 1976. *Handbook of Enzyme Electrophoresis in Human Genetics*. American Elsevier, New York.

Hixon, R. F. 1983. *Loligo opalescens*. Pp. 95–114 in *Cephalopod Life Cycles*, Vol. 1, P. R. Boyle, ed. Academic Press, New York.

Ihssen, P. E., H. E. Booke, J. M. Casselman, J. M. McGlade, N. R. Payne, and F. M. Utter. 1981. Stock identification: materials and methods. *Can. J. Fish. Aquat. Sci.* **38:** 1838–1855.

Kashiwada, J., and C. W. Recksiek. 1978. Possible morphological

indicators of population structure in the market squid, *Loligo opalescens*. *Calif. Dept. Fish Game Fish Bull.* **169:** 99–111.

Lamarck, C. 1798. Extrait d'un mémoire sur le genre de la *Sèche*, du *Calmar* et du *Poulpe*, vulgairement nommés, polypes de mer. *Bull. Société Philomatique Paris* **2:** 129–131.

Lange, A. M. T., and M. P. Sissenwine. 1980. Biological considerations relevant to the management of squid (*Loligo pealei* and *Illex illecebrosus*) of the northwest Atlantic. *Mar. Fish. Rev.* **42**(7–8): 23–38.

Lange, A. M. T., and M. P. Sissenwine. 1983. Squid resources of the northwest Atlantic. *FAO Fish. Tech. Pap.* **231:** 21–54.

LeSueur, C. A. 1821. Descriptions of several new species of cuttlefish. *J. Acad. Nat. Sci. Philadelphia* **2:** 86–101.

Mainland, D., L. Herrera, and M. I. Sutcliffe. 1956. *Statistical Tables for use with Binomial Samples—Contingency Tests, Confidence Limits, and Sample Size Estimates.* Department of Medical Statistics, New York University College of Medicine, New York. 83 pp.

Mesnil, B. 1977. Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*, from the northwest Atlantic. *ICNAF Res. Doc.* **76/VI/65:** 55–69.

Nei, M. 1972. Genetic distance between populations. *Am. Nat.* **106:** 283–292.

Nevo, E., A. Beiles, and R. Ben-Shlomo. 1984. The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. Pp. 13–213 in *Evolutionary Dynamics of Genetic Diversity*, G. S. Mani, ed. Springer-Verlag, New York.

d'Orbigny, A. 1845. Mollusques vivants et fossiles. 1. Paris.

Romero, M. C. L., and T. Amaratunga. 1981. Preliminary results of biochemical-genetic population structure study of the squid *Illex illecebrosus*. Third annual meeting of the Northwest Atlantic Fisheries Organization. *NAFO SCR Doc.* 81/IX/103. Serial No. N405.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. IV. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *Univ. Texas Publ.* **7103:** 49–90.

Shaw, C. R., and R. Prasad. 1970. Starch gel electrophoresis of enzymes—a compilation of recipes. *Biochem. Genet.* **4:** 297–320.

Smith, P. J., P. E. Roberts, and R. J. Hurst. 1981. Evidence for two species of arrow squid in the New Zealand fishery. *New Zealand J. Mar. Freshwater Res.* **15:** 247–253.

Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman & Co., San Francisco. 776 pp.

Summers, W. C. 1971. Age and growth of *Loligo pealei*, a population study of the common Atlantic Coast squid. *Biol. Bull.* **141:** 189–201.

Summers, W. C. 1983. *Loligo pealei*. Pp. 115–142 in *Cephalopod life Cycles*, Vol. 1, P. R. Boyle, ed. Academic Press, New York.

Verrill, A. E. 1882. II. Report on the cephalopods of northeastern coast of America. Pp. 211–455 in *Report to the Commissioner, 1879*. Part VII. U. S. Commission of Fish and Fisheries.

Whitaker, J. D. 1980. Squid catches resulting from trawl surveys off the southeastern United States. *Mar. Fish. Rev.* **42**(7–8): 39–43.